# Taxonomy and Morphology of the Ligulate Species of the Genus Desmarestia

A Thesis Submitted to the Faculty of the Graduate School of the University of Minnesota

by

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# Taxonomy and Morphology of the Ligulate Species of the Genus Desmarestia*

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## 1. INTRODUCTION

In a preliminary paper on the north Pacific coast species of Desmarestia, the writer (Pease, 1917) discussed briefly the principal characters of the genus, and described five species which she had collected in the San Juan Islands. The paper proposed two or three changes in classification, eliminated one species, and inserted *D. tabacoides* Okamura, which had previously been reported only from Japan.

The present paper deals with the taxonomy and morphology of the ligulate species of the genus. Reproducing material of these species has not been collected in the San Juan Islands, and the writer is not yet ready to discuss the functions of the various tissues.

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## 2. Taxonomy

### *a. General*

The genus Desmarestia was established by Lamouroux in 1813, in his masterly "Essai sur les Genres de la Famille des Thalassiophytes non articulées", and as outlined by him consisted of four species, *D. aculeata* (L.), *D. viridis* (Muell.), *D. ligulata* (Lightf.) and *D. herbacea* (Turn.). Agardh (1824), the celebrated Swedish algologist, adopting a different, but no less scholarly system of classification, grouped the four species which Lamouroux had placed by themselves, with several others under the genus Sporochnus. Agardh sub-divided his genus Sporochnus into two groups according to external appearance, the filiform and the plane, putting Lamouroux's *D. aculeata* and *D. viridis* in the filiform group, and *D. ligulata* and *D. herbacea* as the only members of the plane group. Postels and Ruprecht (1840) classified the filiform species as Desmarestia and the plane species as Desmia, the latter a genus name proposed by Lyngbye (1819) to take the place of Lamouroux's Desmarestia, but severely criticised by Greville (1830). Subsequent writers have seen fit to retain Lamouroux's genus Desmarestia with Agardh's sub-divisions.

Naturally with increased facilities for exploration and collection, and for study, numerous additions have been made to both groups of the genus. The present paper, dealing with the ligulate species which occur on the north Pacific coast of America, includes four species: *D. ligulata* (Lightf.) Lamour., *D. herbacea* (Turn.) Lamour., *D. latissima* Setch. and Gard. in litt. n. sp., and *D. foliacea* n. sp.

### *b. Desmarestia ligulata* (Lightfoot) Lamouroux

(Plate 54, Figs. 1, 2; Plate 62; Figs. 1-7; Plate 63.)

| | | | |
|---|---|---|---|
| *Fucus ligulatus* | Lightfoot | Flora Scotica 946. | 1777 |
| | Smith | English Botany, t. 1636 | 1790 |
| | Goodenough | Linn. Trans. 3: 123. | 1797 |
| *Fucus herbaceus* | Hudson | Flora Anglica p. 582. | 1798 |
| *Fucus ligulatus* | Lightfoot | Nereis Britannica, (App.). | 1801 |
| *Fucus herbaceus* | Esper | Icones Fucorum 7:118 | 1808 |
| | Turner | Hist. Fuc. 2:74. pl. 98 | 1809 |
| *Laminaria ligulata* | Hooker | Flora Scotia, Part 2. 99. | 1821 |
| *Sporochnus ligulatus* | Agardh | Sp. Alg. 1:158. | 1821 |
| | | Syst. Alg. 261 | 1824 |
| | Greville | Flora Edinb. 287. | 1824 |
| | Sprengel | Syst. Veg. 4:330. | 1827 |

| | | | |
|---|---|---|---|
| *Desmia ligulata* | Lyngbye | Hyd. Dan. 33, pl. 7 | 1819 |
| | Postels and Ruprecht | Illust. Alg. 13. | 1840 |
| *Desmarestia ligulata* | Lamouroux | Ess. 25. | 1813 |
| | Greville | Alg. Brit. 37 pl. 5. | 1830 |
| | Kützing | Phyc. Gen. 343. | 1843 |
| | Agardh, J.G. | Sp. Gen. Ord. Alg. 1.2.1. 165. | 1843 |
| | Harvey | Phyc. Brit. pl. 115. | 1846 |
| | Hauck et Richter | Phyc, Univ, 420. | 1886 |
| | De Toni | Syl. Alg. 3:460. | 1895 |

*Desmarestia ligulata* (Lightf.) Lamour. was first described by Lightfoot (1777) in the Flora Scotica as follows: "Fronde plana, avenia, subtriplicato-pinnata: ramis ramulisque distischis; foliis lineari-lanceolatis, spinoso-dentatis." Turner (1809) describes the type species as "frond cartilaginous, flat, almost nerveless, doubly pinnate; segments linear-lanceolate, serrated at their margins with spinous teeth." He also describes two forms: "$\beta$ angustior has its frond trebly pinnated, and nowhere above two lines wide; the teeth of its ramuli are so small and obsolete as to be scarcely observable without a glass, whence the whole plant has a naked appearance.' "Y dilatatus, which is a native of more southern seas, is distinguished from the specimens of our coasts by the width of its branches, extending to four lines or more: its ramuli are nearly elliptical, and remarkably attenuate at their base, so that they seem to be supported upon very short petioli."

These three forms have not been kept separate, the difference in growth habit being accounted for, no doubt, by difference in age or vigor of individual specimens.

Turner's description, which is the most complete of those of the early writers, calls attention to the irregular form of the holdfast; the almost cylindrical base of the stipe; the narrow, flattened thallus, with branches of various lengths, "the lowest generally longest, the upper ones regularly shortest, but long and short mostly mixed together, all opposite and undivided, but pinnated with others still smaller, arranged in the same manner, and these occasionally with a third series....." These branches are "attenuated at their base and apices" and "separated by intervals of two or three lines." This species was known to all the early European collectors, but was first collected on American shores on the coast of British Columbia by Lyall, and identified by Harvey (1862). Harvey, however, considered that this and the following species were identical, remarking that "some of the specimens are of ordinary breadth; others are of the widest variety constituting the *D. herbacea* of authors." Setchell and Gardner (1903) quote Harvey, and remark that very few, if any, of the

plants which they have examined correspond to the slender form from European waters.

This narrow form, corresponding to the descriptions of the European type, has been collected for years by members of the Puget Sound Biological Station, on the rocky shores off Kanaka Bay, on the seaward side of San Juan Island. The writer has examined specimens in the Station herbarium and in private collections, and in the summer of 1918 was fortunate enough to secure an abundance of excellent material. The plants were growing on the most exposed point of a steep rocky headland, where strong tidal currents continually sweep along shore, and the heavy surf or ground swell from the open Strait of Juan de Fuca continually breaks on the rocks. Collections were made by hand, with the greatest difficulty, at extreme low tide, as the plants were anchored to the perpendicular faces of great rocky ledges where they were continually submerged, even during the lowest tides.

Early English writers describe the species as varying from two to six feet in length, about 60 cm. to 2 m., but the writer found no specimens exceeding 60 cm. However, the main axis and all the longer branches were, without exception, frayed at the ends, due no doubt to the beating of the plants against the rocks by waves and currents.

The holdfast is not smoothly conical, as in other species examined, but roughly lobed, not only around the circumference, but also over the upper surface, and is much larger than in other species. From about the center of this rough, irregular holdfast arises a single frond with stipe almost cylindrical at the base, but widening immediately, or within 2 or 3 cm. at the most, into a flattened thallus. The main axis reaches an extreme width, in the fresh plant, of 6-8 mm., and is closely and regularly pinnated, at distances varying from 2-8 mm., with opposite distichous branches, which vary extremely in length. Short branches alternate with long without definite sequence, although in general the larger branches are toward the base. Usually both branches of a pair reach about the same stage of development, barring accident, indicating some correlation in growth. The shortest branches are simple, from a few millimeters to one or two centimeters in length, dentate along their margins and comparatively few. From these simple structures up to the longest branches, which may be 30 to 50 centimeters long, and several times pinnate, all degrees of development are found. Branches of all orders narrow down to a slender cylindrical base, and taper to a long point at the extremity. The margins of all the pinnules are sharply and finely dentate, the teeth bearing, early in the spring, tufts of slender branching filaments which are shed later in the season. Toward the base of the frond the midrib is very prominent. In fresh or formalin material it stands out as a distinct

thickening throughout almost the entire length of the main axis and the larger branches and is visible to the unaided eye as a definite ridge on the surface of branches of the third and fourth orders which are only a centimeter long. In herbarium material it is much less evident.

Reproduction has not been observed, but probably takes place as Kuckuck (1894) and Rosenvinge (1894) have reported for *D. aculeata*, and Skottsberg (1907) for *D. firma*.

### c. *Desmarestia herbacea* (Turner) Lamouroux
(Plate 54, Fig. 3; Plate 60, Figs. 1-4.)

| | | | |
|---|---|---|---|
| *Fucus herbaceus* | Turner | Hist. Fuc. 2:78. pl. 99. | 1809 |
| | Mertens | Linnaea. 4:62. | 1829 |
| *Desmarestia herbacea* | Lamouroux | Ess. 25. | 1813 |
| | Greville | Alg. Brit. syn. 40 | 1830 |
| | Kützing | Phyc. Gen. 343 | 1843 |
| | Grünow | Novara 51 | 1867 |
| | Skottsberg | Antarkt. Meeresalg. 23. | 1907 |
| | Pease | P. S. M. S. Publ. 1:388. | 1917 |
| *Sporochnus herbaceus* | Agardh | Syst. Alg. 261. | 1824 |
| | Sprengel | Syst. Veg. 4:329 | 1827 |
| *Desmia herbacea* | Postels and Ruprecht | Illust. Alg. 13. | 1840 |
| | Reinsch | Flora. n.r. 46:189. | 1888 |
| *Desmarestia ligulata var. herbacea* | Agardh,J. G. | Sp.Gen.Ord.Alg. 1.2.1. 169. | 1848-51 |
| | De Toni | Syl. Alg. 3:460. | 1895 |
| | Set. & Gard. | U. Cal. Pub. Bot. 1:247. | 1903 |
| | C., H. & Set. | P.B.-A. Fasc.D. 79 a. and b. | 1905 |

This beautiful species, brought from the northwest coast of North America by Menzies, was first published by Turner (1809) under the name *Fucus herbaceus*, with the following description: "frond membranacea, plana, obsolete costa, bipinnata; segmentis oppositis, ellipticis, base attenuatis, apice obtusis; margine spinoso dentatis."

The writer can formulate no better description of the growth habit of the plant than given by Turner, which is quoted in full. "Root, a small callous disk. Frond flat, two feet or more long, rising with a single individual stem, at its base nearly cylindrical, and as thick as a crow's quill, but almost immediately becoming flat, and gradually widening to the height of a few inches, where it acquires a width of half an inch, or three quarters of an inch, after which it continues linear till, on approaching the extremity, it is again slightly narrowed and terminates in a rounded apex;

the margins are throughout the whole length serrated with small spiniform, rather remote teeth; the stem, from root to summit, is pinnated with opposite distichous branches, of the same substance as itself, between horizontal and patent, separated by intervals of about half an inch, a foot or a foot and a half long, and the middle ones apparently longest, their greatest width nearly an inch, attenuated at their bases into very short subcylindrical petioli, rounded at their apices, toothed at their margins, and in their turns pinnated with a series of others, similar to them in every particular, except their small size; throughout the whole frond runs a midrib thick and rather wide in the stem, but in the branches thin and faint, so as scarcely to be visible, unless the plant is held to the light, and appearing only like a dark line."

He compares this new species with *D. ligulata,* setting forth very clearly his reasons for considering it a distinct species. Postels and Ruprecht (1840) also discuss the specific differences. J. G. Agardh, (1848), however, placed *D. herbacea* as a variety under *D. ligulata* and was followed by other systematists, including De Toni (1895) and Setchell (1903). Harvey (1858 and 1862) went so far as to consider *D. herbacea* merely a broad form of *D. ligulata.* Grünow (1867) again raised the question of specific difference, supported by Skottsberg (1907); and the writer (Pease 1917), in a preliminary paper, published *D. herbacea* as a distinct species. In this discussion, however, all of the forms too broad to be included with the typical *D. ligulata* were considered as belonging to the species *D. herbacea* (Turn.) Lamour. In the present paper the writer wishes to correct that statement, limiting the species *D. herbacea* to those forms which correspond exactly with Turner's original description, and setting apart the larger, broader forms in a group by themselves.

As thus limited, the specimens distributed by Collins, Holden and Setchell (1905), P.B.-A. 79 a. and b., under *Desmarestia ligulata* f. *herbacea,* would belong here.

During the summer of 1918 an abundance of material was collected. which corresponds remarkably with Turner's description and plate. These plants were collected in the same locality and at the same time as the specimens of *D. ligulata.* No intermediate forms were found. The two species were absolutely distinct. A glance at the mass of fronds as they lay floating in the water was sufficient to identify the plant. In color, in width of frond, and in texture, there was no possible room for doubt. The same outstanding differences are manifest in formalin material and herbarium specimens. Anyone who has seen the two plants together could not possibly doubt their identity as distinct species. The two plants are of about the same size. The writer has not collected a specimen of either species which had attained a meter in length. *D. ligulata* is darker in

color, with a greenish tone; has a narrow thallus, not exceeding 6-8 mm. in the widest parts; and has a firmer, heavier texture, with the midrib much more prominent in the older basal portion of the plant. *D. herbacea* is lighter in color, a yellowish brown, with a comparatively broad thallus, 10 to 30 mm. wide; and a much thinner, more delicate texture.

*d. Desmarestia latissima* Setchell and Gardner in Litt. n. sp.

(Plates 55, 56, 57; Plate 58, Figs. 1-4; Plate 60, Figs. 5-9; Plate 62, Figs. 8-10.)

Fronde magna, foliacea, latissima, inferne sub-coriacea et evidenter costata; pinnis distantibus, margine dentis distantibus.

Plant body very large, length up to 8 m.; frond membranaceous, subcoriaceous at base, foliaceous, very wide, diam. 4-100 cm.; with an evident midrib and lateral veins; occasionally bipinnate; pinnae and pinnules widely separated, either blunt or pointed, with margins coarsely spinulose-serrate; veins branching from the midrib, giving off secondary branches which break up into fine veinlets and form a network in the broad thin tissue of the lamina, visible to the eye in both fresh and dry material as faint branching lines.

The species name is credited to Drs. W. A. Setchell and N. L. Gardner of the University of California, who were kind enough to furnish the writer with a brief outline of their provisional arrangement of the Pacific coast species of the genus Desmarestia. Type specimens are deposited in the Alga Herbarium of the University of Minnesota.

The writer believes that this species should be set off from *D. herbacea* on account of its extreme size and the heavier, coarser texture of the thallus; also because it has fewer branches, more widely separated, and only in rare instances do the lateral branches bear branches of the second order.

The species, as designated, includes a wide range of forms, and further study may make it necessary to subdivide still more or at least to segregate one or two varieties, but up to the present time a sufficient number of examples have not been examined and compared so that definite limits can be set, and it is not the writer's intention to split up the genus unnecessarily.

In a series of 25 young plants collected by the writer the length of the main axis varies from 1 to 50 cm. and the width from 0.2 to 13 cm. While in general an increase in width accompanies one in length, the two are not proportional. In these young plants the number of pairs of lateral branches varies from 2 to 14, without any apparent relation to the length or width of the main axis from which they arise. These lateral branches vary in length from 0.5 to 22.5 cm., and in width from 0.2 to 8 cm.

In a series of 58 mature specimens the variation in length of main axis is from 23 cm. to 8 m., and in width from 4 to 40.5 cm. Increase in length seems to have no relation to increase in width. These mature plants bear from 3 to 24 pairs of lateral branches, the number of pairs seemingly having no relation to the length or width of the main axis. The lateral branches vary in length from 21 cm. to 2.5 m., and in width from 3.5 to 23 cm. Table 1 gives some idea of the variation among mature plants. It is evident that it would be exceedingly difficult to find a point where a division could be made on the basis of width of frond.

The specimens of *Desmarestia ligulata* (Lightf.) Lam. var *herbacea* (Turn.) J. Ag., distributed by Tilden (1898), belong here. She includes part of a young plant of the narrow form, and also one of medium width.

Table 1. *Desmarestia latissima, mature, with holdfasts, tabulated according to length of main axis.*

| | MAIN AXIS | | LATERAL BRANCHES | | |
|---|---|---|---|---|---|
| | length cm. | width cm. | No. of pairs | length cm. | cm. width |
| 1. | 55.+ | 10. | 6 | 69. | 15. |
| 2. | 78.+ | 5.5 | 21 | 54.+ | 13. |
| 3. | 100.+ | 10. | 12 | 24. | 5. |
| 4. | 127.+ | 6. | 18 | 58. | 8. |
| 5. | 137.+ | 13. | 17 | 48. | 9.5 |
| 6. | 165.+ | 5.5 | — | — | — |
| 7. | 182.+ | 6.5 | 11 | 24. | 3.5 |
| 8. | 188.+ | 12. | 12 | 117.+ | 16. |
| 9. | 195.+ | 10. | 12 | 50. | 8. |
| 10. | 200.+ | 16. | 3 | 14. | 5.5 |
| 11. | 206.+ | 10. | 14 | 50.5 | 7.7 |
| 12. | 228.+ | 14. | 10 | 154. | 15. |
| 13. | 248.+ | 29. | 11 | 255. | 14.5 |
| 14. | 295.+ | 9.5 | 13 | 77. | 7.3 |
| 15. | 303.+ | 10. | 17 | 63. | 9. |
| 16. | 319+ | 11. | 14 | 41. | 6. |
| 17. | 344.+ | 10.5 | 15 | 91.+ | 9.5 |
| 18. | 383.+ | 17. | 12 | 121. | 12. |
| 19. | 448.+ | 13.5 | 16 | 95. | 11. |
| 20 | 800.+ | 17. | — | 136. | 18. |

Superficially, this species is distinguished from *D. herbacea,* which it most resembles, by its extreme size. Specimens of typical *D. herbacea* have not been collected in the San Juan Islands with fronds longer than one meter, nor wider than 3 cm., and all the specimens collected were of about the same size and general appearance. Specimens of *D. latissima* with fronds up to 8 meters in length and 40 cm. in width were collected by the writer during the summer of 1918; several specimens were found in the summer of 1916 from 40 to 60 cm. in width, and during that same summer Muenscher (1917) collected one specimen 1 m. wide. Setchell and Gardner (1903) mention plants of *D. ligulata* f. *herbacea* "cast ashore at Esquimalt, B. C., in fragments several meters long and full 30 cm. wide." Rigg (1912) says it "sometimes reaches a length of 8 to 10 feet and a width of from 12 to 16 inches (about 3 m. long and 30 to 40 cm. wide—*Author*), although it is usually much smaller." The figures given apply to the main axis of the plant. This axis bears opposite lateral branches which may attain a length of 2.5 m. and a width of over 20 cm.

The lateral branches begin to appear quite close to the holdfast, are at first small and rather crowded, but soon become farther apart and much longer. Well developed branches are usually separated by from one to three pairs of spines, which are merely abortive branches. Practically all of the lateral branches are borne within one meter of the holdfast, plants 3 and 4 meters long having no more branches than those from a meter to a meter and a half in length (table 1). The same thing is true also of young plants, those with a main axis measuring less than 10 cm. bearing as many branches as plants four times as long. Also the main axis usually attains its maximum width within one meter of the holdfast. The occurrence of wider intervals between the upper branches is due to two factors: (1). A larger number of abortive branches between the long branches; (2). Greater elongation of the thallus of the main axis between the branches of the midrib, which form the midribs of the lateral branches.

Abortive branches vary from short sharp spines to flattened outgrowths 3 to 4 cm. long and several mm. wide, which give no external evidence of venation, and do not bear spines along their margins. Normal branches, especially on the narrower forms, are sometimes no larger, but have a definite midrib with visible lateral branches which run out to spines along the margins.

An occasional plant was found in which one or two of the lower pairs of lateral branches were themselves branched, but this is not common and seems to take place when the main axis has been broken off rather close to the holdfast, a phenomenon which reminds one forcibly of the growth habits of higher plants.

In common with other ligulate species, a distinct midrib runs the length of the main axis and gives off at regular intervals opposite branches which extend to the edge of the frond and end in the spine-like teeth, or passing through the attenuate bases of the lateral branches, become the midribs of these structures, giving off in turn pairs of opposite branches which extend to the margins. The midrib is much thickened in the basal portion of the thallus. It also forms a ridge that can be felt with the finger in the basal portion of the long branches.

The one outstanding difference between this species and *D. herbacea,* aside from the extreme difference in size, lies in the system of fine veins which ramify through the laminae of the main axis and the lateral branches. These veins do not originate from the midrib, but are given off as secondary outgrowths from its pinnate, lateral branches. They are given off singly, at irregular intervals, both above and below, branch repeatedly, and form a loose, irregular network in the lamina. The whole effect reminds one strongly of the venation of a long narrow pinnately-veined leaf. Kützing (1858) indicates this method of venation in his plate of *D. herbacea* f. *latior.*

Young plants ranging in length from 10 mm. to 50 cm. seem to show that relative width of frond is determined from the beginning. Some are relatively wide, with long wide branches, the branches equaling or exceeding the main axis, while others are relatively narrow, with short, narrow branches. These represent the extremes of the type however. In both young and mature plants a fairly complete series has been secured, and there seems to be no break in the progressive increase in width of the thallus which would form a basis for dividing the species into two, or even for segregating a form or variety. A factor which complicates the situation is that entire plants have not been found. Even in the smallest specimens secured, the tipe of the long strap-like axis is worn away, so that the real length of the plant in proportion to its width can not be ascertained.

### *e. Desmarestia foliacea* n. sp.

(Plate 58, Figs., 5-10; Plate 61, Figs. 1-5.)

Fronde latissima, ligulata, simplici, tenui stipitata, tenuissime membranacea, margine irregulariter sinuata dentataque, dentibus distantibus, costa media tenuissima et ramosa opposite percursa, ramis se ramulosis, omnibus patentissimis, subtilissimis.

Plant body comparatively small, up to 1 m. long; frond thin, membranaceous, wide, strap-like, diameter to 15 cm.; unbranched; margins irregularly sinuate with occasional obscure teeth; midrib evident, with

opposite branches which break up into fine veinlets. The species name is given on account of the resemblance of the simple frond to a long narrow pinnately veined leaf.

Type specimens are deposited in the Alga Herbarium of the University of Minnesota.

In a preliminary paper the writer (Pease, 1917) described and figured a series of plants collected during the summer of 1916, which she referred to *D. tabacoides,* first described by Okamura (1908) from material collected in southern Japan. Okamura describes his new species thus: "Fronds very large, leaf-like, shortly stipitate, with broadly oval, very usually obliquely lobed, simple, midribbed, and coriaceous lamina. The midrib is slightly prominent below, but gradually becoming fainter upwards, with opposite veins which dissolve, even from the base, into numerous fine veinlets..... The outline of lamina is of large oval shape..... with the length of 30-70 cm. and breadth of 20-50 cm." The description is accompanied by an excellent plate. Since publishing the article referred to, the writer has had the privilege, through the kindness of Dr. W. A. Setchell of the University of California, of examining an authentic herbarium specimen of Okamura's plant. She detects the following differences: 1. The oblique lobing which Okamura mentions in his description. Plants collected on the American coast have sinuate margins with obscure teeth rather widely separated, while the Japanese specimens were "very usually obliquely lobed." 2. The opposite veins, "which dissolve even from the base, into numerous fine veinlets." These are close together, and all their branches come off at very acute angles, corresponding to the "erect branching" of some of the filiform species, and take the same general direction toward the margin of the frond; while in American material the secondary branches are given off more nearly at right angles and have a more definitely reticulate appearance. The distance between the pairs of opposite veins seems to vary with the size, and hence the age, of the specimen. 3. The stipe seems to be much more slender in American specimens. 4. The frond, which in Japanese material is of a large oval shape and reaches a breadth of 20-50 cm., is long and strap-like in American specimens, and not over 15 cm. wide, so far as known.

The description of *D. pinnatinervia* given by De Toni (1895) applied so well to both Japanese and American specimens that the earlier literature was consulted. *D. pinnatinervia* was first described by Montagne (1842) with the comment, "a single specimen collected in 1823 on the coast of Spain, in the harbor of San Sebastian and for a long time considered as a Laminaria." He describes the new species as follows: "Frond stipitata tenuissime membranacea margine denticulis distantibus instructa nervo

pertenui longitudinali aliisque transversis oppositis parallelis percursa." The characteristics which finally decided him to remove the plant from the genus Laminaria and consider it as the type specimen of a new species of Desmarestia were the presence of: 1, a definite stipe; 2, a median vein which extends throughout the length of the frond and gives off opposite lateral branches. The colored plate which accompanies the description shows the same general growth habit as the Japanese and American specimens, i. e., a broad, flat frond, unbranched, with a median vein which gives off opposite lateral branches, the latter branching again. It does not, however, give the details of the venation, only one secondary branch from each lateral vein being shown.

Agardh (1848), who according to Montagne, had examined the original specimen, lists it under "Species inquirendae" with the remark, "Videtur pars inferior frondis latioris Desmarestiae ligulatae." His description, "Fronde latissima plana costate simplice, margine edentato serrata, in stipitem attenuata," varies somewhat from Mantagne's and may have been either from the specimen itself or from Mantagne's plate.

Kützing (1849) must have written his description from the plate, as the phrase "costis apice bifurcatis" would indicate, the plate showing only one secondary branch from each lateral vein and no finer subdivisions. De Toni (1895) quotes Kützing's description, adding Agardh's comment concerning its resemblance to *"D. ligulata* var. *firma."*

Johnstone and Croall (1859) close their discussion of *D. ligulata* by saying, "Under the present species we would place the form *D. pinnatinervia,* our impression being that they are identical; although at first sight the great breath of the frond, and the very narrow and distinct pinnated nerve, would indicate a distinct species." Although claiming to have specimens collected in the north of Ireland, they give no plate, and the species is not mentioned by other writers in lists of British marine algae.

It would seem then, that all authentic published accounts of this species are based on Montagne's and Agardh's opinions of a single specimen, Kützing apparently having written his description from Montagne's plate and De Toni having quoted Kützing and Agardh.

Until specimens of the three can be placed side by side for comparison, the most that can be said is that the Japanese, the American, and the Spanish plants resemble each other very closely, and if not three very closely related species, are three forms of the same species.

The ligulate species of the genus Desmarestia should be further subdivided, then, into two groups, one to include the branched forms, the other the simple forms. It was this unbranched condition of the frond which caused Montagne to hesitate for nearly 20 years before finally classifying

his plant as a Desmarestia, and then he did so with the comment: "Si c' est un Desmarestia, comme tout le fait croire, on peut considerer la fronde entière comme formée par la soudure des pinnules opposées que representent les nervures."

A few specimens of the proposed new species, *D. foliacea,* were secured during the summer of 1916, and referred at the time to *D. tabacoides* Okamura. In the summer of 1918, while collecting over the same ground, an abundance of material was secured in all stages, from plants 2 or 3 cm. long up to those about a meter in length.

In very young plants, the lateral veins can be traced unbranched to the margin of the frond, and a few of these young plants have been collected which still show the protruding stubs where the assimilating hairs have broken off. In older specimens, however, the margins are sinuate, with obscure teeth rather widely separated, and the lateral veins which branch out from the midrib do not appear to extend to the edge of the lamina, as in other ligulate species, but break up into a fine branching network. The lateral veins stand almost at right angles with the midrib, and their branches, in turn, are almost at right angles. These secondary branches subdivide again and again, the finer branching being followed easily with a hand lens. This visible network of fine veinlets in the lamina relates the species closely to *D. latissima.* In fact, except for its extreme thinness, a plant of *D. foliacea* bears a remarkably close resemblance to a lateral branch of *D. latissima.*

The writer has not seen reproducing material. Okamura (1908), in his discussion of *D. tabacoides,* describes and figures plurilocular sporangia intermingled with sterile hairs, in sori forming irregularly roundish patches on both surfaces of the lamina. To the writer these bear a close resemblance to a species of Phycocelis which she has found growing on the fronds of several species of Desmarestia (Plate 60, Figs. 1, 2, 3). In the light of work done by Rosenvinge (1894), Kuckuck (1894) and Skottsberg (1907), on reproduction in various species of Desmarestia, it is highly probable that Okamura's interpretation is not correct.

### *f. Key to Species*

In accordance with the ideas expressed in the preceding pages, the author wishes to present the following scheme of classification, which affects only the ligulate species of the genus Desmarestia which appear in the Puget Sound region, with the exception of *D. pinnatinervia* Mont. and *D. tabacoides* Okamura, which are introduced for the purpose of comparison.

A. Frond much flattened, blade-like; midrib evident (ligulate species).
  B. Frond unbranched.
    C. Stipe short (4-5 mm.), heavy; secondary veins not pronounced ..... *D. pinnatinervia* Mont.
    CC. Stipe long (10-20 mm.), heavy; secondary veins pronounced, appressed ..... *D. tabacoides* Okam.
    CCC. Stipe long (8-16 mm.), slender; secondary veins pronounced, at about 90 degrees ..... *D. foliacea* n. sp.
  BB. Frond branched.
    D. Branches of first and occasionally second order; plant body large, with main axis up to 1 m. wide, 8 m. long. *D. latissima* Setch. and Gard. in litt. n. sp.
    DD. Branches of third and fourth orders; plant body small.
      E. Fronds up to 8 mm. wide. *D. ligulata* (Lightf.) Lamour.
      EE. Fronds 10-30 mm. wide. *D. herbacea* (Turn.) Lamour.
AA. Frond terete or compressed, not flattened; midrib not evident. (Filiform species).

### 3. Morphology

#### *a. Historical*

There are two types of thallus in the genus, represented by *Desmarestia aculeata* and *D. ligulata.* In the *D. aculeata,* or filiform type, the main axis and all its branches, to the last order, are slender and terete, or only slightly compressed, with the axial filament and its surrounding tissues, the so-called midrib, not at all evident from the surface. In the *D. ligulata,* or ligulate type, the main axis and all its branches are much flattened, with a very evident midrib. The latter type, the ligulate group, represented on the Pacific coast according to the opinion of the writer by four species, will be considered in the following discussion.

The general growth habit of all species studied is the same, and has already been worked out by various writers. The plan of the present writer has been to gather together from many scattered sources and to summarize the work already done and then to add the results of her own observations.

The plant is attached to its substratum, which may be a rock, a shell, or the holdfast or stipe of another alga, by means of a simple disk-shaped or flattened-conical holdfast. From the center of the holdfast arises a single round or slightly compressed axis which begins to widen out within 1 or 2 cm. into the ligulate thallus. The main axis may remain unbranched, as in *D. foliacea,* or may bear branches to the fourth order, as in *D. ligulata.* Lateral branches are opposite, distichous, patent to erect, with

serrate margins, and begin to appear not more than 2 or 3 cm. above the holdfast.

The mature parts of the frond are differentiated into several tissue systems. The main axis, together with all its branches of all orders, is traversed by a single row of cells, the axial filament or rachis, surrounded by an inner assimilation tissue of small cells, the whole forming the so-called "midrib." Surrounding this, and forming the main substance of the broader parts of the thallus, is a ground tissue consisting of very large cells, among which ramify slender filaments containing scattered chromatophores. The whole plant body is covered by a cortical layer from one to three cells thick.

The entire young plant and the younger parts of old plants are clothed during the active growing season in early spring, with opposite, distichous rows of monosiphonous branching filaments, which give the plant a most beautiful feathery appearance. The cells of the filaments are crowded with chromatophores and according to Söderström (1889) can be considered as assimilatory organs which have an important bearing on the rapid development of the young twigs.

According to Janczwski (1875), lateral and terminal filaments are the same in structure and can be distinguished only by their position. They are either simple or branched and the main filament and its branches develop basipetally, the outermost cells being the oldest and in his opinion the most vigorous. On account of the fact that one finds younger, shorter branches among the older ones, Söderström reasons that the cells of the rachis divide transversely and the new cells thus formed also send out branches. The branches originate as opposite outgrowths from the upper part of cells of the rachis. These become cut off from the parent cell by a cross wall, elongate, divide transversely, and increase in length by repeated transverse divisions of the basal cell formed by their first transverse division.

Toward the end of the growing season the hairs break off just above the growing region and are shed bodily. Their bases remain as small thorn-like projections along the sides of the thallus twigs, gradually become covered by the growth of the cortical cells, and persist in the form of serrations or small thorn-like "short branches."

The growing region, as in many other Phaeophyceae, is intercalary, lying between the thallus and the hair-like filaments, and giving off cells to each. According to Jönsson (1901) the first two or three cell divisions in the growing region are necessarily apical, but by subsequent divisions of the inner cells the growing region becomes intercalary. The earliest stages of development have never been observed, but the development of the various tissues can be followed in the growing tips of the fronds.

The newest part of the thallus is a single row of articulate cells, lying just below the growing region, which bears opposite distichous branches at frequent intervals. According to Söderström, each original cell of the monosiphonous thallus below the growing region bears opposite branches, which must therefore stand very close together. This is not the case for long, however, as observation will show that at a short distance below the growing region the segments bearing branches are separated by a distance the length of three cells, showing that the original segment cell, through successive divisions, has given rise to four cells. Söderström says that no further division of the segment cells takes place, only an elongation to keep up with the growth of the thallus, as repeated observation shows branches arising from every fourth cell.

According to observations made by Reinke (1880) and confirmed by Söderström, the cortical cells arise as outgrowths from the axils of opposite lateral branches of the monosiphonous thallus at some distance below the growing region. By repeated transverse divisions these outgrowths, instead of developing as hair branches, form filaments which are applied to the axial cell. These filaments, encircling the axial cell, meet and fuse, and by repeated divisions form a layer of small cells surrounding the original single cell row of the thallus. To the writer it would seem that the idea expressed by Jönsson is more nearly correct, namely, that from the bases of opposite lateral hairs cells are cut off which, by repeated divisions, form a girdle about the central cell. Repeated examination of the growing tips of three different species, both in cross section and from the surface, gave no indication of the development of filaments which were applied to the axial cell.

When the axial cell has become completely enclosed, the cells of the investing layer, or cortex, divide tangentially, forming a surrounding tissue two cells thick. The inner layer, immediately surrounding the central axis, is the beginning of the ground tissue, and from it, later, through secondary growth, develops the "inner assimilation tissue." The outer layer remains permanently meristematic, cutting off by repeated tangential divisions cells which are added to the ground tissue, and dividing radially to accommodate the increasing size of the thallus. According to Jönsson the cells of the ground tissue never increase their number by division, the increase is always by addition from the outer meristematic layer. The cells of the ground tissue become very greatly enlarged in length and diameter, are smaller at the extremities, with their ends lapping past each other, and in older parts of the frond the walls are considerably thickened.

According to Harvey (1858), the manner of growth in *D. ligulata*, which is typical of the ligulate forms, is precisely similar to that in the filiform species, "except that the new cellular integument to the primary

filament is not developed equally on all sides, but extends chiefly laterally, so as to form first a two-edged and then a flat or even leaf-like stem. In this process of lateral extension, or widening of the stem, the lower portions of the pinnae of the primary filament, being enclosed within the cellular wings of the flattened branch, become the lateral nerves of the frond."

The outer cells remain small and are crowded with small lens-shaped chromatophores, thus forming the principal assimilating region of the plant. The cells immediately within the outer cortical layer are somewhat larger, the chromatophores are less crowded, and the protoplast becomes peripheral, having within it a single large vacuole in which the nucleus is suspended by slender strands of cytoplasm. The cells rapidly increase in size toward the center and the chromatophores rapidly decrease in number and finally disappear, though the large cells of the ground tissue remain nucleated after all trace of chromatophores has vanished. Thus it can be seen that in the primary tissues only the three or four outermost layers of cells of the thallus are engaged to any appreciable degree in photosynthetic work.

At the end of the period of elongation, then, which occurs early in spring, the newly formed thallus consists of three primary tissue regions: (1) The axial row of cells formed from the primary growing region, which bears regular opposite distichous branches; (2) The cortical region, consisting of two or three layers of small isodiametric cells densely filled with chromatophores. The outermost layer remains permanently meristematic, cutting off cells laterally to accommodate the increasing width and length of the thallus, and dividing parallel to the surface to add to its thickness. The inner cortical cells enlarge to form (3) the ground tissue, composed of greatly enlarged cells with bluntly tapered ends in which the protoplasm is distributed as a very thin peripheral layer within which a few scattered chromatophores may be imbedded.

At about the close of the growing period, which is marked externally by the shedding of the filamentous hairs and the complete cortication of the thallus, the formation of secondary tissues begins. This includes the "inner assimilation tissue" and the "conducting hyphae" which ramify through the intercellular spaces of the ground tissue. The tissue of small cells which completely surrounds the original thallus cells of the axial row, called by Söderström the inner assimilation system, is described by him as consisting of several layers of extremely small, thin-walled, endochrome-containing cells which originate by repeated oblique divisions in all directions of the cells of the ground tissue which lie next to the central cell. Söderström is at a loss to explain the presence of chromatophores deep within the thallus. But Wille (1895), under whose direc-

tion he carried on this work, explains in a later article "the peculiar appearance of an inner assimilation tissue," assuming that lively respiration goes on in the large protoplasm-filled cells of the central cylinder, and that the $CO_2$ formed in this way is taken up immediately in sunlight by the inner assimilation system, while the outer assimilation system makes use of the $CO_2$ absorbed from the surrounding water. This arrangement he considers necessary because of a lack of either stomata or intercellular spaces, as in higher plants, to facilitate gas exchange.

Söderström also described and figured cross sections of the thallus from near the holdfast, where "certain cells of the ground tissue" had also become surrounded by a system of very small thin-walled cells which had the same appearance as those of the inner assimilation system. Jönsson, by means of diagrammatic longitudinal sections, proves that the central cell of that group does not belong to the ground tissue, but is formed by secondary branching of the lateral branches of the central axis; these secondary branches, arising from the lower side of the lateral branches, grow downward toward the base of the plant between the cells of the ground tissue, and become surrounded, like the cells from which they originate, by a tissue of small assimilation cells.

Jönsson calls Söderström's inner assimilation tissue a "secondary assimilation tissue" and describes a "tertiary assimilation tissue" in the older parts of the thallus. This is formed by outgrowths from the secondary assimilation system which pierce the walls of the central cylinder cells and form within the cell cavities a dense mass of hypha-like growths. These divide by cross walls to form small, closely packed cells which contain many chromatophores and therefore aid in assimilation. If Wille's assumption as to the necessity for the secondary assimilation system be correct, one wonders how the formation of this tertiary system can be explained on the basis of function?

The conducting hyphae, as described by Söderström, also originate from the cells of the ground tissue. They seldom arise in young parts of the thallus, but develop gradually, with the growth of the plant. In older parts they are found penetrating everywhere between the cells of the ground tissue, so that the latter may become widely separated. The hypha first appears as a sac-like outgrowth from the side of a cell of the ground tissue, is cut off from the parent cell by a cross wall, and elongates by terminal growth. Cross walls are formed as growth progresses. It forces its way among the cells of the ground tissue, twisting and turning, but keeping its course steadily downward toward the base of the plant. These hyphae branch repeatedly and twist and turn about themselves and about the cells of the ground tissue until it is impossible to follow a single hypha for any distance through the tangled mass. Since their growth is steadily

downward, the lower parts of the thallus are made up almost entirely of this tangled mass of hyphal threads, the original cells of the ground tissue having been pushed widely apart by them. They continue down through the base of the stipe and into the holdfast, where they spread radially, and form the main bulk of the disk. In the basal portions of the plant, where they constitute most of the substance, their walls are much thickened, according to Söderström, and their function is almost entirely mechanical.

### *b. Methods*

The foregoing summary is intended to present in a concise form what is already known of the structure and development of the thallus in the genus Desmarestia. Practically all morphological work has been done with *D. aculeata* as the basis for study. Since this was the first member of the genus to be recognized and described by the early systematists, is the most widely distributed species, and seems to be at least fairly common throughout its entire range; it is not surprising that it has received more attention than other species of the genus, and that its structure as worked out by Kützing (1843), Janczewski (1875), Reinke (1880), and especially by Söderström (1889) and Jönsson (1901), should be considered as typical. But since the type of thallus in the two groups of the genus is so entirely different it is natural to suppose that there would be at least minor differences in the formation and development of the various tissues, if not in their structure. The writer has studied the structure of *D. aculeata* (L.) Lamour., *D. viridis* (Muell.) Lamour. and *D. media* (Ag.) Grev. among the filiform species; and *D. ligulata* (Lightf.) Lamour., *D. herbacea* (Turn.) Lamour., *D. latissima* Setchell and Gardner in lit., n. sp., and *D. foliacea* n. sp. among the ligulate species. The work done on the filiform species was for the purpose of verification and comparison, and will not be discussed in the present paper. Microphotographs of cross and longitudinal sections through the mature part of the thallus of *D. aculeata* are given (Plate 61, Figs. 6 and 7) so that the size, shape, and distribution of cells may be compared with those of the ligulate species. Reproducing material has not been collected in Puget Sound waters, and the writer will not attempt to discuss reproduction.

All material used was collected in the San Juan Islands in July 1916 and July 1918, and preserved in 2% formalin in sea-water. As wanted for study since, the material has been removed from formalin, cut into pieces of suitable size, dehydrated by running up slowly through a close series of alcohols, and imbedded in paraffin, using both xylol and cedar oil as solvents. Sections were cut from 10 to 15 micra in thickness, and stained with Bismarck brown. Most of the material was stained after sectioning, but toward the end of the work a few slides were made by

staining in bulk and afterwards sectioning and mounting. The results were very satisfactory. The material is easy to handle; any good method carefully followed brings the desired results. Drawings were made with the camera lucida or with projection apparatus.

Chlorzinciodide was used to determine the composition of the cell walls. Formalin material was rinsed in tap water and the concentrated reagent was applied directly, to flat pieces of the entire thallus, to pieces stripped of the cortical layers, and to sections. The cell walls of both primary and secondary tissues gave the characteristic violet coloration of cellulose. Both Söderström (1889) and Jönsson (1901) recognize the marked resemblance of the cells of the central cylinder to the sieve tubes of higher plants, but neither is willling to concede that they are true sieve tubes, though Jönsson figures and describes the pores in the cross walls and the protoplasmic connections extending through them. Both chlorzinciodide and Bismarck brown distinctly show the presence of callose covering the sieve plate in older parts of the frond, and in younger stages the progressive development of the callose covering is clearly shown. The callose is first formed as a ring at the outer edge, on both sides of the sieve plate, and gradually extends inward across the plate, finally forming a complete covering, through which, in some cases, the pores can be traced. The original cell row of the thallus, then, is a row of sieve tubes, as are all of its branches and their subdivisions. The system of veins which forms a delicate though clearly visible network throughout the fronds of the extremely broad species is thus a system of sieve tubes.

*Desmarestia ligulata,* the type species of the ligulate group, has been used as the basis for study. A detailed description of the formation and development of the thallus and its various tissues will be given, and the three remaining ligulate species, *D. herbacea, D. latissima,* and *D. foliacea,* will be compared with it.

### *c. Desmarestia ligulata* (Lightfoot) Lamouroux

(Plate 54, Figs. 1, 2; Plate 62, Figs. 1-7; Plate 63.)

Although collected in midsummer, some of the material still bore assimilating hairs, so that all stages in the development of the thallus could be observed,—the structure of the hairs themselves, the intercalary growing region, the beginning of cortication, the development of the axial filament; in fact, the formation and development of primary and secondary tissues from the tip of the youngest thallus branch to the base of the holdfast.

Söderström (1889) says of the hairs of *D. aculeata,* "Their cells contain much chlorophyll, they are closely and regularly branched, and up to 3 cm. long." In *D. ligulata* the hairs are very much shorter, be-

ing visible to the naked eye only by the filmy appearance which they give to the edges of the ultimate pinnules. They are set much more closely together and hence do not appear to be in tufts, as Oltmanns (1904) illustrates them for *D. aculeata* (Plate 59, Fig. 1). Many of the hairs, especially those arising near the base of the pinnule, are short and simple, and of less diameter than the more vigorous branched hairs toward and at the distal end. The main axis of the hair, formed by cells cut off form the upper side of the intercalary growing point, may consist of from 10 to 50 cells. The hair is spindle-shaped. The youngest cells, next the growing point, are about 100 micra wide and 15 or 20 micra long. The largest cells, about its middle, are 125 to 200 micra in diameter and 175 to 225 micra long. The tip ends in a small conical cell about 37 micra wide at the base and 45 to 70 micra long. The individual cells are slightly distended in the middle, and thus barrel-shaped.

In branched hairs, the branches arise as outgrowths on the sides of the cells of the main axis, which are soon cut off by cross walls. A cell thus cut off divides again and the branch elongates by repeated division, this always occurring in the innermost cell, so that the hair branch develops basipetally. These branches, like the axis from which they grow, are spindle-shaped, with a conical end cell. Although the lateral branches of the central axis below the growing point always arise in pairs, and both members of the pair persist, so that branching is always opposite, the lateral branches above the growing point quite often arise singly, and several single branch hairs in succession may be produced, either on the same or on opposite sides of the axis (Plate 62, Fig. 1). In fully grown hairs, both proximal and distal ends of the axis, which are respectively the youngest and oldest regions, are devoid of branches, while in the intermediate region branches are closely crowded. In this crowded region every cell, or every second or third cell, bears a pair of branches, or occasionally only a single branch. Usually, from 3 to 10 cells of the axis bear branches, and the first 10 to 15 cells at the distal end of the axis are devoid of branches. The branches themselves consist of from 5 to 15 cells each and do not branch again, as they sometimes do in *D. aculeata.*

The writer has examined the assimilating hairs in *D. aculeata* and *D. viridis* as well as in *D. ligulata,* and finds that the size and shape of the cells and also the arrangement of the branches is different in each species. It would be interesting to examine the assimilating hairs of other species. It may be possible that this could be made one of the distinguishing characters in separating species.

At the end of the growing season all the assimilating hairs are shed, a definite method of abscission being quite apparent. Entire pinnules were stained in Bismarck brown, cleared in cedar oil, and mounted in balsam. The tissues are so transparent that one can focus through the cortical layers

of the midrib, trace its lateral branches out to the edge of the cortex, and note their continuation, through the short cells of the intercalary growing point, into the axis of the assimilating hairs. Just at the edge of the cortex, the basal cell of the assimilating hair and the outer cell of the midrib branch round away from each other at their separating wall, making the axis thinner at this point and therefore weaker. The hair breaks off at this weak point and the cortical cells, by lateral divisions, soon cover the broken stub, leaving a blunt projection on the edge of the pinnule (Plate 62, Figs. 2 and 3).

Renewal of growth has not been observed in *D. ligulata,* but in *D. media* (Ag.) Grev., collected in the same region in April 1917, the first cell of the assimilating hair was just protruding through the cortex at the tips of many of the ultimate branches.

At the same time that the assimilating hairs are being developed the central axial row of cells of the midrib, the "original thallus" of Janczewski (1875), is being increased in length by the addition of cells from the lower side of the intercalary growing point. These cells, almost as soon as formed, send out projections on either side which are cut off by cross walls and develop into lateral branches. Branches of the axial row above the growing point may or may not be in pairs, and do not develop from every cell; but in the permanent axial row below the growing point, every cell that is cut off bears two opposite branches. The axial cell elongates below leaving the branches on its upper part, and divides by a cross partition, the branches being on the upper cell. Each of these cells elongates and again divides. Thus the pair of branches will be found on the uppermost of the series of four cells formed by two successive divisions of the original cell laid down at the growing point. Sőderstrőm (1889) states that in *D. aculeata* no further divisions take place in the cells of the axial row, every fourth axial cell throughout the thallus bearing branches. Each axial cell, therefore, must become greatly elongated to keep pace with the elongation of other tissues of the thallus. In pinnules of *D. ligulata,* well cleared and not too deeply stained, the writer has been able to trace the axial row for 3 or 4 millimeters. Branches arise from every second, third or fourth cell, but no wider intervals have been observed. The same holds true for longitudinal sections of older parts of the thallus. Each original cell does not necessarily subdivide to form four cells. For instance, in the basal region of a branch of the first order, branches have been found on every second axial cell, indicating that only one division has taken place. In other sections, every third axial cell bears branches (Plate 59, Fig. 2), indicating that the original cell and one of the daughter cells has divided. When every fourth cell bears branches, it is evident that both daughter cells of the original axial cell have again divided. No greater intervals between lateral branches have been found in any part of the thallus, hence

cell division in the axial row probably takes place in *D. ligulata* in the same way that Söderström has already demonstrated for *D. aculeata.*

Since the original wall which cut off the branch cell was not perpendicular to the transverse wall of the axial cell, but slightly oblique to it, the branch, at its beginning, was not exactly at a right angle but inclined slightly forward toward the growing point. The lateral walls of both axial cells and lateral cells in the young stages are not cylindrical but barrel-shaped. As a result, the supper side of the basal cell of the branch is pressed against the base of the axial cell next above, and the two walls become adherent. Subsequent changes in the shape and position of the cells due to the development of surrounding tissues so modify their appearance at the point of juncture that unless the early stages were traced it is impossible to tell from which axial cell the branch originates (Plate 62, Figs. 2 and 3, and plate 59, Figs. 2, 3 and 6).

Cortication begins immediately below the growing point, and according to the observation of the writer does not proceed as indicated by Reinke (1880), who claims that filaments develop which become applied to the axial cell, encircle it, meet and fuse, and by repeated division form a layer of small cells lying close to each other about the original cell of the thallus. The cortical layer originates, as described by Janczewski (1875) and Reinke (1880), as a small cell cut off on the lower side of the basal cell of a lateral branch of the main axis. This new cell does not divide again immediately, but another small cell is cut off from the side of the same basal cell. The first cell to be cut off then divides, either below or on one side. Since the same process is proceeding on the opposite side of the hair branch, a cluster of small cells is thus formed about its base. Meanwhile, the opposite branch hair of the pair is also developing a cluster of small cells about its base. At this time there is then a cluster of small cells on opposite sides of the axial cell, and this is the beginning of the flattened thallus. The axial cells at this point have a length only about half their diameter, and each cell bears a pair of branches, hence the branches are very close together, and the cluster of small cortical cells about the base of one lies in contact with the branch below it. These cortical cells now divide laterally without any definite sequence, and gradually spread toward each other until the axial cell and the basal cells of its paired branches are completely covered (Plate 63).

Since elongation of the axial row is taking place at the same time, several stages of this process of cortication can be observed on a single filament. From the point at which the first small cell is cut off to the point at which complete cortication is attained, from two to six axial cells may intervene, in all intermediate stages of cortication.

By the time complete cortication is reached, the basal cells of the

branches of the axial filament, from which the first cortical cells were cut off, have elongated and the adjoining cells have divided. The growing region of the branch hair is thus moved outward, so that branches below the growing point of the main axis have intercalary growth, while branches above the growing point, as previously explained, develop basipetally (Plate 62, Figs. 1 and 2). The dividing cortical cells extend outward along the bases of the lateral branches, as well as around the axial cells, so that when the axial cells have one layer of cortical cells covering their lateral walls between the paired branches, there is a flat extension of cortical cells surrounding and between the bases of the successive lateral branches which is two or three cells broad. Division of cortical cells in the plane of the lateral branches proceeds quite rapidly, the cells of the axial filament elongate and divide, and there is thus formed a flat thallus consisting of a filament of large cells bearing distichous branches, the whole covered by a single cortical layer of very small cells. The lateral branches increase in length by addition of cells at the intercalary growing point, and the cortical growth spreads outward, keeping the branches covered almost to their growing points.

At a distance 4 to 6 axial cells behind the point where complete cortication is effected, the cortical cells have begun to divide parallel to the surface of the thallus, thus forming the beginning of the ground tissue. A few cells farther back, another parallel division has taken place, the inner cell of the first division having greatly enlarged meanwhile, accompanied by the rapid division of the meristematic outer cortical layer in a plane perpendicular to the flat surface of the thallus, to keep pace with its rapid increase in length and width. In a small pinnule well stained and cleared one can focus through the successive layers of cells and make out their size, shape and arrangement very distinctly. At this point all the cells of the thallus still contain chromatophores, the small cortical cells of the surface layer being densely crowded with them, while the rapidly enlarging cells of the ground tissue still have a few scattered through the layer of peripheral protoplasm. They are also present in the axial cells.

As Jönsson (1901) says, there is no definite point at which primary growth stops and secondary growth begins. The material used in this study still bore assimilating hairs, though most of them had been shed. Cortication was still in progress at the tips of some of the pinnules, while the formation of the secondary assimilation system had already begun farther back toward their bases.

In focusing down through the superficial walls, the inner assimilation system first appears as a series of long slender filaments lying alongside the large cells of the axial filament. In cross section the axial filament appears to be surrounded, or partly surrounded, by small cells (Plate 62, Fig. 6). In longitudinal section, the filaments can be seen originating

in the large cells of the ground tissue. When the filaments first begin to elongate, cross walls are rather infrequent, the cells of the filaments having a length of from 2 to 5 times their diameter (Plate 62, Figs. 3, 4, 5). Intercalary cross walls soon appear, the filaments become more numerous and begin to twist and turn about the central axis and about each other as they force their way along the path of least resistance toward the base of the pinnule. In this way a mass of small cells is formed about the axial cells (Plate 59, Figs, 2-5). The filaments making up this assimilating tissue elongate not by elongation of the individual cells, which remain small and pratically isodiametric, but by apical growth, the end of the filament elongating and forming cross walls.

The "conducting hyphae" of Söderström originate in the same way as the inner assimilation tissue, as outgrowths from the large cells of the ground tissue. Söderström says that the cells of the ground tissue never divide, but any increase in their number is by addition from the cortical meristem. The writer has found all degrees, from the elongation of the entire cell with formation of cross walls, forming a chain of several large cells which gradually narrows to a small filament, down to small slender outgrowths from the end or side of the ground tissue cell. The hyphae vary exceedingly in diameter, and branch repeatedly, forming a tangled network which binds the cells of the ground tissue firmly together, making the lamina a tough pliable sheet.

Inner assimilation tissue and conducting hyphae have the same origin and both develop in the same way. The only structural difference seems to be that in the first hyphal filaments formed, which surround the axial cell row, intercalary cross walls are formed which divide the filament into small isodiametric cells, while in the hyphal filaments formed later, and farther from the axial cell row, intercalary cross walls do not appear, the filaments being made up of long cylindrical cells. Moreover, the major part of the conducting hyphae are developed immediately surrounding the inner assimilation tissue. In *D. aculeata,* according to Söderström, "the inner assimilation tissue consists of five or six layers of very small, thin-walled, endochrome containing cells," while in *D. ligulata* there are only one or two layers of small iso-diametric cells containing chromatophores, which are surrounded in turn by a zone of conducting hyphae of varying width, depending upon the age of the portion of thallus examined, and the region of the plant body from which it is taken (Plate 59, Figs. 2-6).

In the mature thallus the cells at the outer edge of the lamina are younger, hence are smaller and have produced less of the hyphal growth. The cells surrounding the axial row and its covering of small assimilating cells produce more of the hyphal growth than do the cells of the flat lamina; thus causing a thickening of the thallus, and producing the evi-

dent midrib which characterizes all the ligulate species. This would account also for the increased thickness of the midrib toward the base of the thallus (Plate 59, Fig. 4).

In the short cylindrical stipe and the slender petiole-like bases of the branches, very few ground tissue cells were laid down originally, and the number is not increased from year to year. The greater part of the tissue in these regions is made up of hyphal filaments which follow down the main axis of the thallus or of its lateral branches.

Jönsson (1901) was the first worker who correctly interpreted the origin and structure of the secondary inner assimilation systems which appear in the basal portions of the thallus of old *D. aculeata* plants. He shows, by means of diagrammatic longitudinal sections, that the axial cell row originates as a branch, growing down from the lower side of one of the basal cells of a lateral branch of the main axial strand. This branch elongates, growing downward among the cells of the ground tissue, and be comes covered with layers of small cells containing chromatophores, in the same way as does the main axial strand. This same secondary development occurs in all the ligulate species of the genus, but is carried out on a much more extensive scale.

It was brought out earlier in the discussion that while the lateral branches of that portion of the axial filament above the intercalary growing point develop basipetally, the permanent branches below the growing point increase in length by means of an intercalary growing point which is formed after cortication begins, and which remains always at the edge of the flat thallus. Just as the original cells of the main axis may by repeated division form 2, 3, or 4 cells, so the cells of the permanent branches also increase in number by repeated divisions. This is especially noticeable at the base of the branches, where division takes place so rapidly that a series of short cells is produced. It will be remembered that originally the lateral branches are inclined at an angle a little less than 90° from the main axis. During this period of elongation and rapid cell division in the lateral branch, the new cross walls formed by the dividing basal cells are laid down parallel with the main axis, so that the basal portion of the branch, as these cells elongate, stands squarely at right angles with the main axis (Plate 59, Figs. 2, 3, 6 and Plate 62, Fig. 3).

It is from the lower side of one of these basal cells that a lateral branch grows out which ultimately becomes the axis of a secondary inner assimilation system. This secondary branch may appear at any point along the lower side of the cell, though it is usually at about the middle, giving the branched cell the appearance of a T-tube. The branch elongates by apical growth and cross walls are laid down back of the growing tip. As the cells thus formed mature, they take on the appearance of typical sieve

tubes, their cross walls give the callose reaction, and protoplasmic connections through the sieve plates can be demonstrated. As the branch develops it becomes invested with a layer of assimilating cells in its older parts, and as it grows downward through the ground tissue of the lamina it may give off branches which in turn acquire an investment of assimilating cells (Plate 59, Figs. 2, 3, 6, and Plate 62, Fig. 7).

It is obvious that these secondary assimilation systems must originate in younger parts of the thallus, before the cells which bear them have become closely invested with assimilating cells and several layers of closely interwoven conducting hyphae. The entire mature thallus is penetrated by these branching systems of sieve tubes surrounded by their assimilating cells, and all in connection, through the lateral branches of the midribs of the pinnae, with the larger branches, and so with the main axis of the compound thallus.

Söderström developed the idea of two secondary tissues originating in the cells of the ground tissue. The foregoing discussion shows that the axial cells of the "original thallus" also give rise to a secondary tissue in exactly the same manner. There are thus two systems of secondary tissues, one developing from the original thallus, and the other from the ground tissue which surrounds it.

The holdfast in *D. aculeata,* according to Söderström, is made up in the central part mainly of a mass of interwoven and outspreading hyphae, which function more as mechanical support than for conducting, while the tissue of the peripheral parts is made up of rectangular cells, lying in regular parallel rows. In *D. ligulata* the central tissue of the holdfast is a mass of filamentous hyphae branching and running in all directions between the few cells of the original ground tissue, which have become widely separated by this secondary growth. These hyphae originate not only in the ground tissue among which they lie, but descend along the midrib of the stipe from the ground tissue cells of the lower parts of the frond. Through all this central tissue ramify numerous branching sieve tubes surrounded by assimilating cells, the sieve tubes originating as secondary outgrowths from the lowest branches of the main axis, which naturally forms the central structure of the holdfast, as it does of all other parts of the frond.

In the cortical region of the holdfast, the new cells which are cut off from the inner side of the outermost layer do not enlarge to form ground tissue, but remain of practically the same diameter as the mother cell, although they may elongate somewhat perpendicular to the plane of division. Since several of these cells may be cut off during one season's growth, the resulting tissue has the appearance of a mass of closely packed, roughly parallel filaments.

There is a sharp line of demarcation between the cortical growth of two seasons, which gives the appearance in section of annual rings (Plate 59, Fig. 7). This is due to the fact that the cells first formed in the spring elongate much more than those formed later in the season, while those cells which form the outer cortical layer of the resting season are small and isodiametric, and develop heavier walls.

### *d. Desmarestia herbacea* (Turner) Lamouroux

(Plate 54, Fig. 3; Plate 60, Fig. 1-5).

Neither young plants nor plants bearing assimilating hairs were collected, hence it has been impossible to determine the process of development of the various tissues. However the tissues of the mature plant in the resting condition resemble so closely those of *D. ligulata* that it is natural to suppose that they are formed in the same way.

The increased width of the thallus of *D. herbacea* over that of *D. ligulata* is due to the fact that all primary growth, in older parts of the plant, takes place at the edge of the thallus. The cortical cells in this region divide parallel to the surface of the thallus, and the inner cells develop into ground tissue, while the superficial cells divide rapidly at right angles to the surface to accommodate the increasing width. In the older region of the lamina, nearer the midrib, the only growth is secondary, and consists in further development of the conducting hyphae and sieve tubes.

There are five definite tissue regions in the thin flat lamina of the thallus, the two cortical layers, each underlaid by the large cells of the ground tissue, and between the two ground tissue regions, forming the central layer, a weft of interwoven conducting hyphae, among which ramify the branching sieve tubes (Plate 60, Figs. 1, 2, 3).

It is in the increased development of the sieve tubes of the secondary inner assimilation tissue that *D. herbacea* differs most materially in structure from *D. ligulata*. The secondary branches of the lateral veins, which originate as in *D. ligulata*, continue their growth among the conducting hyphae of the central layer of the lamina, branching and rebranching, without the investment of small inner assimilation cells with which older parts of the system are provided, but themselves containing many chromatophores, as do all young cells of the primary thallus. They are easily distinguished from the conducting hyphae, many of which are of about the same diameter and also contain chromatophores, since in sections lightly stained in Bismarck brown, the ring of callose which is forming about the edge of the sieve plate takes the stain much more deeply than do the cellulose walls (Plate 60, Fig. 1).

*e. Desmarestia latissima* Setchell and Gardner in Litt. n. sp.

(Plates 55, 56, 57; Plate 58, Figs. 1-4; Plate 60, Figs. 5-9; Plate 62, Figs. 8-10.)

Several very young plants from one to five centimeters long were collected, one of which still bore a few assimilating hairs. Not enough hairs were observed to make general statements possible. Those studied were small and sparsely branched; their main axis spindle-shaped and less than 20 cells long; their branches either single or in pairs, tapering at the ends, and composed of from 5 to 8 cells. Several pinnules terminated in unbranched hairs.

As in *D. ligulata* every cell of the permanent central axis, laid down below the intercalary growing point, bears a pair of lateral branches. By subsequent repeated divisions of the original axial cells, these paired branches become separated by a series of up to 8 cells, whereas, in *D. ligulata* not more than 4 axial cells were observed between successive pairs of branches. The cells of the axial row could be counted very easily by focusing down through the superficial cells of entire young plants which had been lightly stained in Bismarck brown.

The young tips of the branches were in the same stages of development as the tips of the pinnules in *D. ligulata*. Cortication proceeds in the same way. At the tips of those branches whose axial cells did not produce hair branches, a pair of lateral cells was cut off, as in the beginning of branch hairs, but these single cells cut off small cells below, then at the side, and cortication proceeded in the usual way, by repeated division of these cells.

In these same plants the beginnings of the inner assimilation tissues were visible as slender filaments made up of cylindrical cells, arising in the cells of the ground tissues and closely applied to the cells of the central axis. Secondary growth from the lateral branches of the central axis was also well under way, the secondary branches themselves branching and ramifying among the cells of the ground tissue.

All these cells in these young plants were extremely small, and lateral branches were very close together. Young plants up to 50 cm. in length bore no greater number of branches, hence a tremendous elongation of the cells of the thallus between the branches must take place.

The structure of the mature thallus does not differ from that of *D. herbacea* except in degree. The lamina consists of the same five tissue regions, developed to a much greater extent, as the enormous width of

the thallus in some individuals testifies (Plate 60, figs. 5-8). The secondary growths of sieve tubes, which in *D. herbacae* ramify among the conducting hyphae, in this species become invested with inner assimilation cells in their older parts (Plate 60, fig. 5), and are visible on the surface of the lamina as the network of veins between the lateral branches of the midrib. Toward the outer edge of the lamina, in the younger tissue, they are still uninvested, and are not visible from the surface.

The cells of the ground tissue are so firmly bound together by the long branching filaments of the conducting hyphae that in formalin material the cortical layers, which become loosened and form large blisters, can be stripped from both surfaces and an entire lateral branch will preserve its original shape and texture, and the veining can be traced as easily as in a skeleton leaf. In plate 62, figs. 8 and 9, is shown the method of branching of the conducting hyphae, while fig. 10 shows how firmly the cells of the ground tissue are bound together by the interwoven meshes of the hyphae.

In studying sections of the stipe and holdfast of a young specimen, a single longitudinal section plainly showed the axial cell row of the midrib or "original thallus" extending through the base of the stipe to the bottom of the holdfast (plate 60, fig. 9); and the covering of assimilating cells, gradually becoming less and finally disappearing at the base of the holdfast. This would seem to indicate that the plant originates as a simple monosiphonous filament which later develops branches and becomes corticated. This is probably true of all members of the genus, as it is the condition found at the thallus tips of all species at the beginning of the active growing season.

*f. Desmarestia foliacea* n. sp.

(Plate 58, Figs. 5-10; Plate 61, Figs. 1-5)

Except for its extreme thinness and delicacy of texture, this species closely resembles a single lateral branch of *D. latissima*. In structure the two are identical. Plate 61, fig. 1 shows a flat section through a younger portion of the lamina, with the large cells of the ground tissue, the interwoven conducting hyphae, and the secondary growth of sieve tubes, not yet surrounded by assimilating cells. The sieve tubes are easily distinguished from the hyphae by the heavy callose rings formed on the cross walls. In fig. 2, from an older part of the lamina, the sieve tubes are surrounded by a layer of small assimilating cells.

In fig. 3, a cross section through the edge of the lamina, the primary growing region of the plant is shown, that is, the region in which new ground tissues are added to older parts of the thallus, the result being an increase in the width of the thallus. The increase in thickness of older

parts of the thallus, aside from increase in size of the original ground tissue cells, is brought about, as stated before, by secondary growth, that is, by continued development of conducting hyphae.

A longitudinal section through the upper part of the stipe of a mature plant is shown in fig. 4. Contrast the length of the portion of an axial cell shown with the length of the axial cells in fig. 5, a longitudinal section through the base of the stipe and upper part of the holdfast in a young plant. Note also in fig. 5 the mass of conducting hyphae surrounding the central axis. In this young plant an inner assimilation tissue had not yet developed, though sections of the same region in mature plants show an abundant development of assimilating cells.

In discussing the structure of his *D. tabacoides*, Okamura (1908) says, "The axis is not composed of a single longitudinal row of cylindrical cells, but of many short filamentous cells, densely packed and firmly coalesced in a very irregular manner." This would correspond to the "tertiary assimilation tissue" which Jönnson (1901) describes in *D. aculeata,* formed by outgrowths from the secondary assimilation tissue, or "inner assimilation" of "Söderström" (1889), which pierce the walls of the axial cells and form dense masses in the cell cavities. The writer has found nothing resembling a development of this sort in any of the ligulate species examined.

### *g. Conclusions*

In the four ligulate species of the genus Desmarestia under discussion, the difference in width and thickness, in venation, and in texture of the thallus is due, not to fundamental differences in structure, but to differences in the relative amounts of primary and secondary tissues, and to differences in the size of the cells of corresponding tissues and the thickness of their walls. A comparison of the figures in plates 59-61 will make this very evident.

In *D. ligulata* there is comparatively little lateral extension of the lamina and an abundant development of conducting hyphae, making a thick and narrow, but very tough and pliable thallus. In *D. herbacea* there is greater lateral extension but less development of hyphal tissue, and hence a broader but much more delicate lamina. In *D. latissima* the lamina is enormously extended, there is comparatively little hyphal tissue, except in the basal portions, but the individual cells are extremely large and thick-walled. There is also an extreme development of secondary branches of the inner assimilation tissue. In *D. foliacea* the extreme thinness of the lamina is due to the fact that it is the minimum number of cells in thickness, and the cells are very thin walled, especially in younger plants, so that when dry there is very little substance.

## 4. Summary

In the taxonomic portion of the paper, the writer has discussed two well established ligulate species of the genus Desmarestia, *D. ligulata* (Lightf.) Lamour., and *D. herbacea* (Turn.) Lamour.; has presented a species recently separated from the latter, *D. latissima* Setch. and Gard. in litt., n. sp.; and has proposed a new species, *D. foliacea* n. sp.

In the discussion of the morphology of these ligulate species, all the available literature has been summarized and the following new points have been presented:

1. The transitory assimilating hairs during the period of elongation in early spring differ in several species examined, and further examination in other species may lead to the conclusion that difference in assimilating hairs can be made to constitute a species difference.

2. The primary axis of the assimilating hair is not regularly branched, but branches may occur singly or in pairs, and are separated by a varying number of axial cells.

3. At the end of the growing season the assimilating hairs are cut off by a definite method of abscission.

4. The cortical layer does not originate as filaments growing out from the basal cells of branch hairs which become applied to the axial cells, but as two groups of cells cut off from the basal cell of opposite paired branches, which divide without definite order and produce a single layer of cells covering the axial cell and the bases of its lateral branches, and so form a flat thallus.

5. There are two systems of secondary tissues: (a). The "inner assimilation system" and "conducting hyphae" which originate from the cells of the ground tissue. (b). The secondary outgrowths from the lateral branches of the axial filament or "original thallus," which in very broad species form a network of veins in the lamina, visible from the surface.

6. The cells of the axial filament and all its branches, both primary and secondary, develop into true sieve tubes.

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## PLATE 54

Figs. 1 and 2. *Desmarestia ligulata* (Lightfoot) Lamouroux. X 0.26.

Fig. 3. *Desmarestia herbacea* (Turner) Lamouroux. X 0.26.

PLATE 54

## PLATE 55

Figs. 1-4. *Desmarestia latissima* Setchell and Gardner showing bases of plants bearing lateral branches of various widths. X 0.20.

PLATE 55

## PLATE 56

Figs. 1-4. *Desmarestia latissima* Setchell and Gardner showing various widths of main axis. × 0.20.

PLATE 56

## PLATE 57

*Desmarestia latissima* Setchell and Gardner. Plants in condition as secured with a trawl. White bar on surface of thallus is 152 mm. (6-inch) ruler. X 0.04.

Fig. 1. Fragment of a plant. Main axis 40.5 cm. wide.

Fig. 2. A small plant attached to the base of the stipe of an older one.

PLATE 57

## PLATE 58

Figs. 1-4. *Desmarestia latissima* Setchell and Gardner. Young plants. X 0.20.

Figs. 5-10. *Desmarestia foliacea*. Plants of various sizes and ages. X 0.20.

PLATE 58

## PLATE 59

*Desmarestia ligulata* (Lightfoot) Lamouroux.

Fig. 1. Tip of branch, showing crowded arrangement of assimilating hairs. X 88.

Fig. 2. Longitudinal section through midrib showing sieve tubes of central axis, surrounded by inner assimilation tissue and conducting hyphae; three pairs of lateral veins, originating from every third cell of central axis; middle pair of lateral veins with secondary branches. X 88.

Fig. 3. Same as fig. 2. X 88.

Fig. 4. Cross section of main axis, showing arrangement of tissues. X 88.

Fig. 5. Cross section of branch of first order, showing central axis with pair of lateral branches. X 188.

Fig. 6. Longitudinal section of branch of second order, showing branching in secondary branches of veins. X 88.

Fig. 7. Section of holdfast, showing two years' growth. X 88.

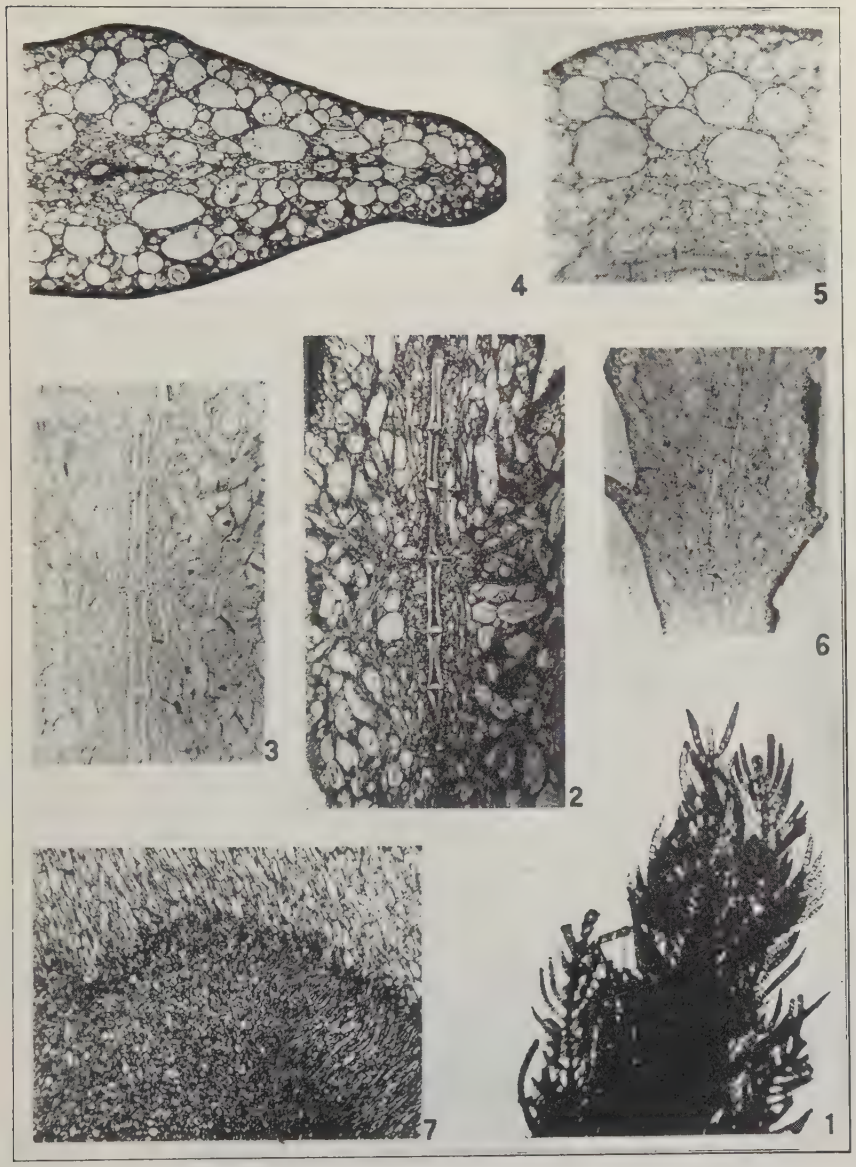



PLATE 59

## PLATE 60

Figs. 1-4. *Desmarestia herbacea* (Turner) Lamouroux.

Fig. 1. Longitudinal section of young tissue, sieve tubes of central axis with beginning of inner assimilating tissue, and branch veins without assimilating tissue; callose at sieve plates. X 88.

Fig. 2. Cross section of lateral branch, through midrib and through lamina. X 88.

Fig. 3. Cross section of lamina of lateral branch. Phycocelis sp. epiphytic on surface. X 188.

Fig. 4. Cross section of thallus, near stipe, with Phycocelis sp. X 188.

Figs. 5-9. *Desmarestia latissima* Setchell and Gardner.

Fig. 5. Cross section of lateral branch, showing sections of small seondary veins surrounded by assimilating cells, large cells of ground tissue and small cortical cells. X 188.

Fig. 6. Longitudinal section of lateral branch, through midrib, perpendicular to flat surface of frond. X 88.

Fig. 7. Cross section of lateral branch. X 88.

Fig. 8. Longitudinal section of midrib, base of main axis. X 188.

Fig. 9. Longitudinal section of holdfast, showing central axis reaching almost to base. X 50.

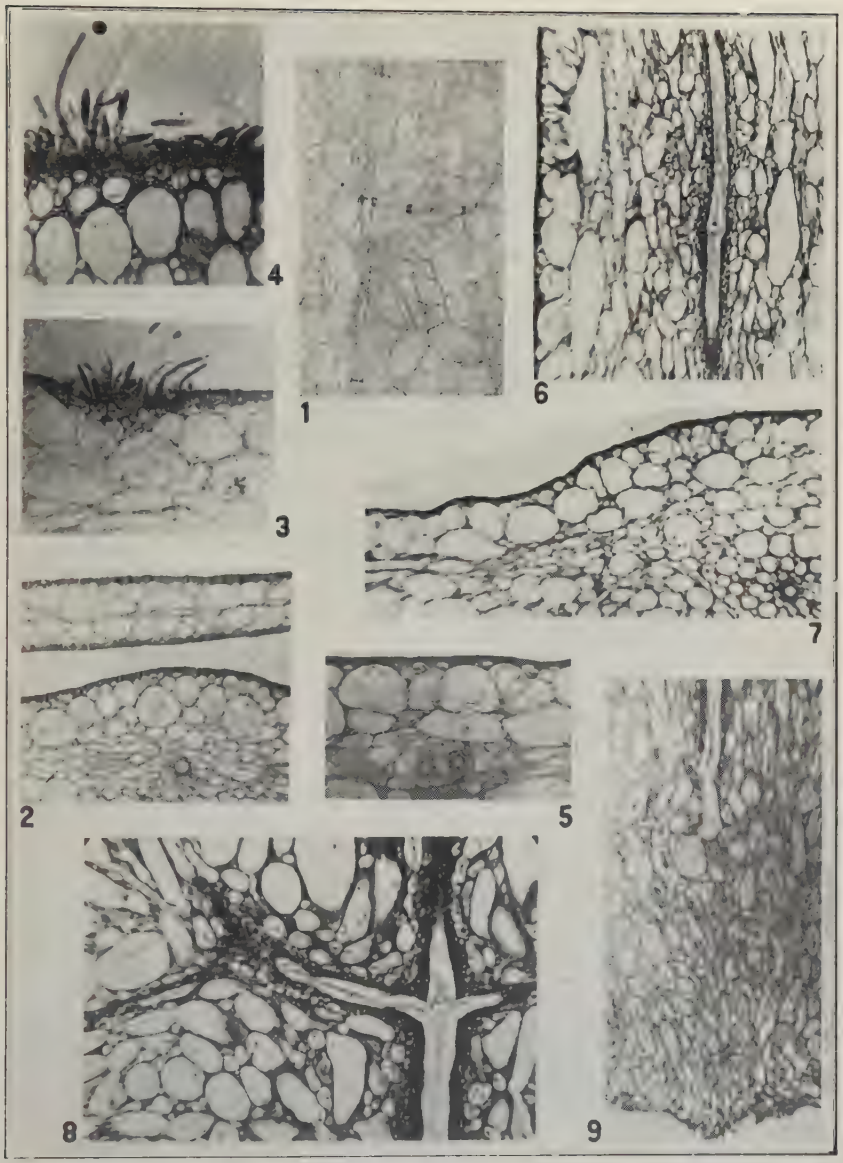



PLATE 60

## PLATE 61

Figs. 1-5. *Desmarestia foliacea.*

Fig. 1. Longitudinal section, showing young secondary veins without investment of assimilating cells, distinguished from conducting hyphae by callose sieve plates. X 88.

Fig. 2. The same as Fig. 1 but of older tissue, showing inner assimilating tissue surrounding secondary veins. X 88.

Fig. 3. Cross section of edge of frond, showing arrangement of tissues and growing region at extreme edge. X 188.

Fig. 4. Base of stipe and central region of holdfast, showing central axis extending into holdfast. X 88.

Fig. 5. Longitudinal section of base of frond, showing central axis with pair of lateral branches surrounded by inner assimilation tissue and conducting hyphae. X 88.

Figs. 6, 7. *Desmarestia aculeata* (Linnaeus) Lamouroux. Longitudinal and cross sections of main axis, showing arrangement of tissues and size of cells as compared with cells of ligulate species. X 88.

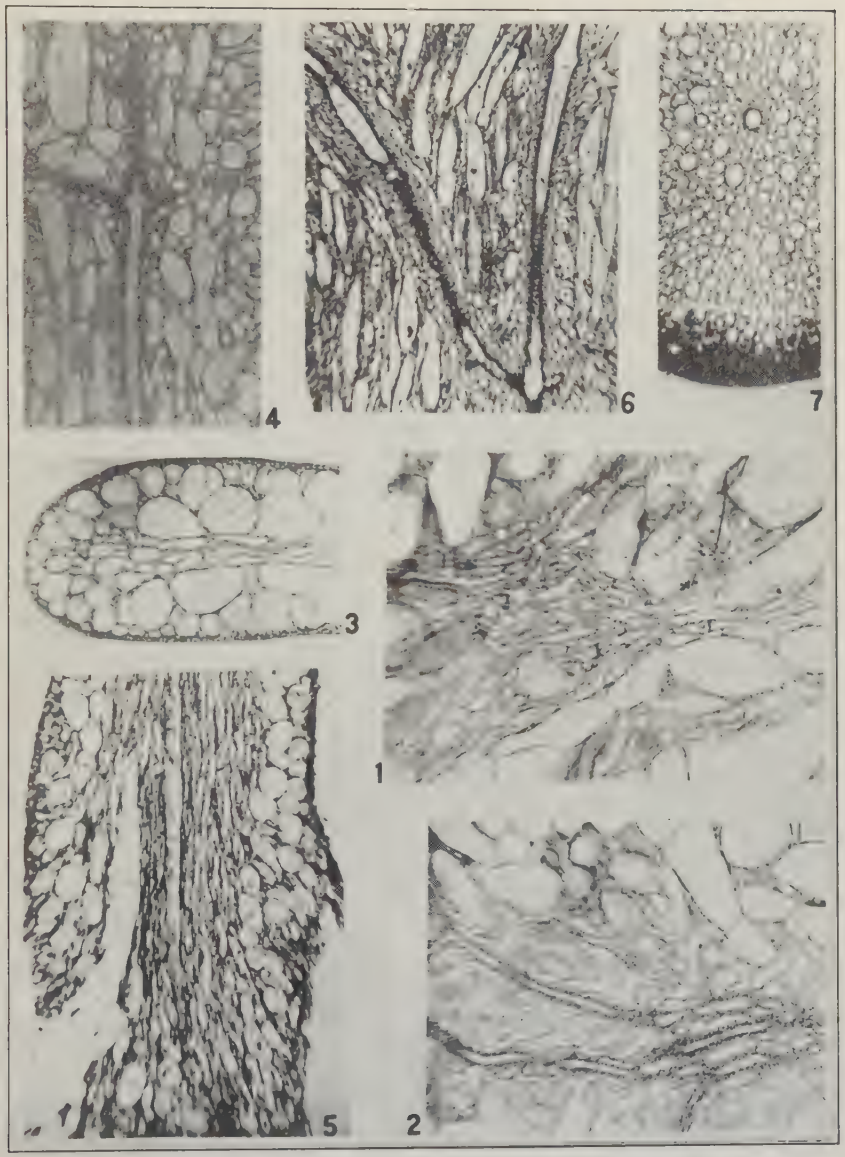



PLATE 61

## PLATE 62

Figs. 1-7. *Desmarestia ligulata* (Lightfoot) Lamouroux.

Fig. 1. Original row of cells of thallus: a, intercalary growing region; b, terminal hair bearing lateral branches irregularly arranged; e, permanent axis with opposite lateral branches. X 275.

Fig. 2. Longitudinal section of young lateral branch: aa', central axis; bb', edge of thallus; c, intercalary growing region of lateral branches; d, point of abscission. X 170.

Fig. 3. Longitudinal section of young lateral branch: a, central axis; b, lateral branch; c, cortical layer; d, ground tissue; e, beginning of development of inner assimilation tissue. X 170.

Fig. 4. Cross section of young lateral branch, such as in Fig. 3. X 170.

Fig. 5. Longitudinal section of young branch perpendicular to flat surface of frond. X 170.

Fig. 6. Cross section of young branch, showing inner assimilation tissue surrounding central axis, and distribution of chromatophores. X 165.

Fig. 7. Branching sieve tube from secondary outgrowth from lateral branch of central axis. X 170.

Figs. 8-10. *Desmarestia latissima* Setchell and Gardner.

Figs. 8-9. Method of branching of conducting hyphae. X 275.

Fig. 10. Network of conducting hyphae with chromatophores, between two regions of large ground tissue cells. X 170.

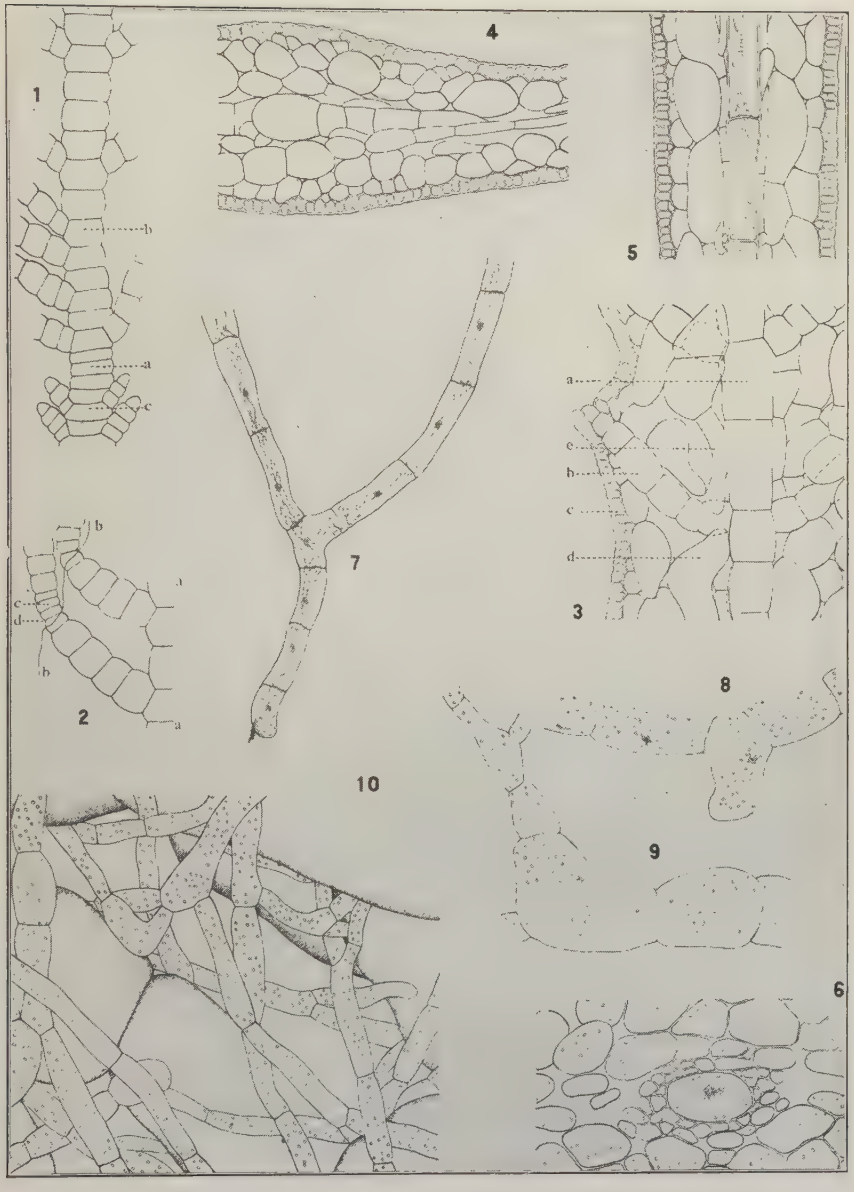
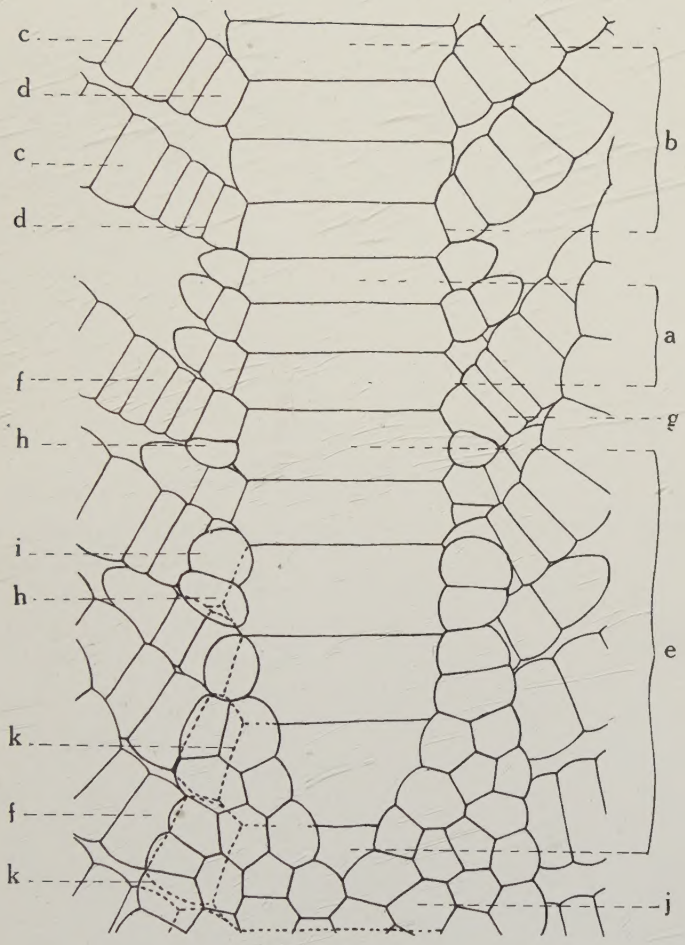



PLATE 62

## PLATE 63

Origin of cortical layer in *Desmarestia ligulata* (Lightfoot) Lamouroux, partly diagrammatic. a, Intercalary growing region; b, Base of terminal hair; c, Bases of lateral hair branches; d, Basal growing region of branches; e, Permanent axis of thallus; f, Bases of lateral branches of permanent axis; g, Intercalary growing region of branch; h, First cell cut off in formation of cortex; i, Second cell cut off in formation of cortex; j, Cortication complete; k, Cells of original thallus covered by cortex.

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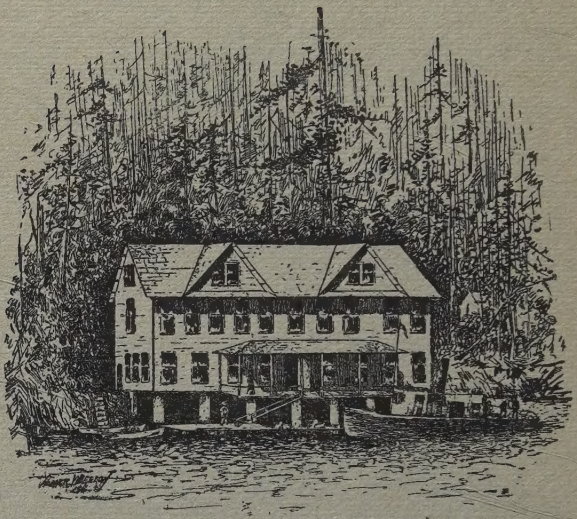

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